Ocean-Dispersed Drift Seeds in Relation to Beach Slope and Particle Size: Fine-Scaled Patterns on a Tropical Shore

by Rojina Nekoonam

Abstract: Arrival of drift seeds on shore following long-distance dispersal by ocean currents is affected by a number of factors, including hydrology and geological processes. Measurements of beach slope and sediment size class and collections of seeds from the high tide drift line were made following high tide at 20 randomly-selected points along a 200-m transect at San Miguel Biological Station, Cabo Blanco Absolute Reserve, on the Pacific coast of Costa Rica. Percent slope was highly variable, ranging from 1.83-12.3%. Sediments were ranked from coarse to fine: cobbles, pebbles, coarse sand, medium sand, and fine sand. Pebbles were most common. Percent slope of the beach was not independent of sediment size; larger particle sizes were found on steeper slopes, and finer particles were deposited at lower beach profiles. Thus, patterns of sedimentology well-documented at continental scales were found to apply even at a very fine scale on this shore. A total of 1049 drift seeds were collected, of which 75% belonged to a single species, *Terminalia catappa* (Combretaceae), "almendro." The number of seeds per sample was highly variable, ranging from 1-391. The species richness per sample ranged from 1-22 (mean 5.7 species), and increased as a function of the number of seeds sampled. Seeds were not distributed independently of one another among samples, but showed a non-random, clumped pattern, tending to occur in clusters more often than expected by chance. Seed length ranged from 0.4-24 cm (mean 4.14 cm). Larger seeds tended to be found at sample sites with larger particle size and with steeper topography; therefore, patterns of seed dispersal on the shore were generally similar to patterns of sediment deposition. Processes shaping beach topography and sediment composition are dynamic, changing with each tide, storm event, and season. Thus, the relationships seen in this study, at one point in time, between beach slope and sediment size and between beach slope and seed deposition, must be constantly re-established over very short intervals.

Intoduction

Seed dispersal involves the movement of seeds away from the parent plant, a process which contributes to genetic outcrossing as well as to the colonization of new sites. Plants have limited mobility and thus rely on a variety of dispersal mechanisms to transport their seeds. Dispersal vectors include animals, which feed on fleshy fruits or carry sticky seeds on their fur, as well as explosive dispersal from seed pods, wind, and water. Long-distance dispersal by ocean currents has been described for seeds that are buoyant and can tolerate extended periods of immersion in seawater (Nathan et al., 2008); these seeds may drift passively with ocean currents for hundreds of kilometers. Adaptations such as small size and light weight, internal air cavities in the seed, waterproof coats, and corklike or fibrous coverings, permit drift seeds to remain afloat for days or even years (Zuchowski, 2005).

The transport of seeds by ocean currents is particularly important for the colonization and growth of vegetation on tropical and subtropical shorelines. Rivers and streams also carry seeds downstream where they may be deposited on tropical beaches (Smith, 1990). It is predicted that deposition of drift seeds on the shore is affected by the same factors that affect deposition of other materials: hydrology, including patterns of ocean currents, tidal cycles, and wave action. Geology, which includes the rocks, particles, and processes that shape the seafloor bathymetry, morphology, and slope of the foreshore, also affects deposition of drift seeds.

Certain processes involving ocean currents and coastal sedimentology are well-established in the literature (Davidson et al., 2002). Waves moving onshore become steep and break in shallow waters, and the breaking waves and resulting currents pick up and move sand particles, shifting sediments and carving out coastlines. Beaches are dynamic; there is constant interaction and feedback between wave action and beach morphology. As waves shape the beaches, the form of the beach, in turn, affects wave action.

According to Davidson et al. (2002), the strength of wave action determines what sediments are deposited. Slow-moving water with little wave energy can only transport the finest particles, while strong waves and currents are able to move all sizes of particles, both small and very large. The natural angle of deposition of water-borne sediments is positively correlated with particle size. The larger the particle size, the steeper is the angle of deposition, such that tidal mudflats deposited by slow moving water are, as the name indicates, flat in profile, while boulder beaches deposited by crashing surf are steep. This paradigm has been useful in contrasting shorelines worldwide with markedly different extremes of wave energy. It is not known whether these patterns can be detected at a fine scale, on the order of a few hundred meters, on a single tropical shore (Davidson et al., 2002).

The shore environment at San Miguel Biological Station, Cabo Blanco Absolute Reserve on the Pacific coast of Costa Rica shows marked heterogeneity in beach morphology (see Figure 1) and the distribution of particle sizes (see Figure 2), even within short distances. This raises the possibility of exploring the variability in sediment patterns and beach slope at this very small scale, and testing whether seed deposition reflects a process similar to that of sediment deposition.

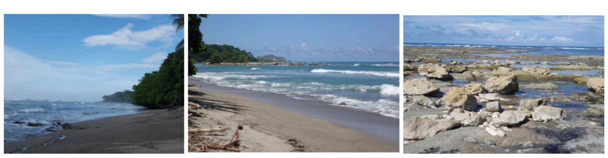

Figure 1. Contrasting beach forms at San Miguel Biological Station, Cabo Blanco. Left, sandy beach with little wave action; center, sandy beach with moderate wave action; right, boulders tossed in the intertidal zone by heavy surf.

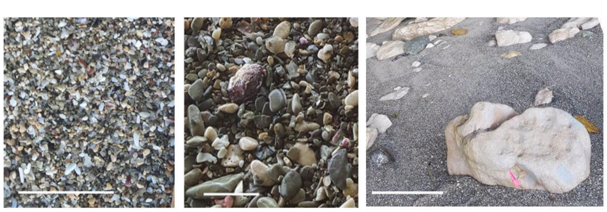

Figure 2. Examples of contrasting particle sizes from beach sediments in the study area. Left, medium sand (scale bar 3 cm); center, pebbles, including limestone (white), turbidite (gray), basalt (black), quartzite (transparent) and shell fragments (scale bar 3 cm); right, limestone cobbles (scale bar 30 cm).

This study aims to address the following research questions: (1) Does the nature of sediment exchange contribute to the shape of the beach and therefore seed dispersal; and (2) Is there variation in how seeds are dispersed along Cabo Blanco's sandy beaches, and do drift seeds arrive in a random pattern? The goal of this study is to assess the relationship between foreshore slope, sediment particle size, and ocean-dispersed drift seeds sampled at a fine scale at San Miguel Biological Station.

Methods

The study was conducted July 11-12, 2018, at the San Miguel Biological Station (9° 35'N, 85 °08'W), Cabo Blanco Absolute Nature Reserve. Located at the southernmost tip of Costa Rica's Nicoya Peninsula, Puntarenas Province, the site receives around 3 m of rain per year, mostly falling in the rainy season from mid-May to mid-November (Camacho Céspedes and Lindquist, 2007). Vegetation is 55-year-old secondary forest, naturally regrown after the Reserve was established in 1963. The vegetation type is dry-moist tropical coastal forest (Camacho Céspedes & Lindquist, 2007). The Reserve is bordered on the west and south by the Pacific Ocean and on the east by the Gulf of Nicoya.

There are two high tides and two low tides per 24 hours on this coast. Tidal amplitude is high; during the study period, the vertical difference between low tide and high tide ranged from 2.4-3.0 m (8-10 ft). At the highest point of each high tide, a clear drift line remains, with depositions of seeds, fruits, small pieces of wood, shells, seaweed, leaves, and a variety of ocean-dispersed trash (see Figure 3).

Figure 3. Left, drift line produced as water retreats following the high tide. Right, detail with leaves, seeds, and twigs. The division between dry sand above the drift line and wet sand below is well defined.

Figure 4. Left, leafy branches of almendro, *Terminalia catappa*, at the edge of the shoreline; almendro fruits lying on the ground are indicated by white arrows. Right, pile of almendro fruits (dark) and seeds (pale).

Preliminary observations of seeds in the drift line at San Miguel showed that the overwhelming majority of seeds belonged to beach almond or almendro, *Terminalia catappa* (Combretaceae); because of its dominance in the seed assemblage, this species became a special focus of the study (see Figure 4). Descriptions of the species (Zuchowski, 2005; Camacho Cespedes & Lindquist, 2007; Condit et al., 2011) indicate that almendro is native to India but is now common worldwide, having been dispersed by ocean currents to all tropical and subtropical shores. The trees are tolerant of strong winds, salt spray, and moderately high salinity environments with sandy soils. Growing well in sandy coastal plains and low-lying areas, they are a dominant species along the shores in Cabo Blanco. The seeds are generally 4-7 cm long, 2.5-3.8 cm wide, pointed at the apex, and flattened, rather like an almond in shape as the common name suggests. The prominent keel around both sides of the seed add buoyancy, allowing it to float for long distances in the sea (Zuchowski, 2005; Invasive Species Specialist Group [ISSG], 2018).

The sampling universe was a 200 m length of beach near the San Miguel station buildings. This stretch was divided into 40 sectors measuring 5 m in length, each marked at its midpoint by a stake flag. Twenty of the forty sectors were drawn at random for sampling. Sites that were inaccessible due to streams or dense vegetation were excluded from sampling. The percent slope of the beach was measured at each flag using a line level, a 5 m length of string, and a meter rule; the angle was then calculated trigonometrically. The substrate was photographed at each site to permit characterization of the particle size of sediments. Five size categories were used (listed from coarse to fine): 1- cobble; 2- pebble; 3- coarse sand; 4- medium sand; and 5- fine sand. If more than one sediment category was present, the most common type at the site was recorded.

Seeds were collected from the drift line during the daytime low tide on July 12th. All seeds present at the randomly assigned sites were collected, placed in a labelled bag, and transported to the laboratory for sorting, counting, and measuring. Fresh-looking seeds that appeared to have recently fallen from the branches overhead were excluded from the samples. For each of the 20 sample bags, the almendro seeds were separated from seeds of all other species, and the two groups of seeds were counted and measured separately. The total number of species in each bag was tallied, permitting analysis of species richness. All seeds were measured in length. To account for broken or fragmented seeds, the following procedure was used: if 50% of the seed was present, it counted as half a seed; if more than 50% was present, it was counted as one seed; and if less than 50% was present, it was discarded without counting.

Results

The slope of the beach measured at 20 randomly sampled points over a 200-m length of beach at San Miguel ranged from 1.8-12.3%, with a mean of 7.00% (see Figure 5). The frequency distribution of sediment size classes at the 20 points is shown in Figure 6. Pebbles were the most frequently observed category.

There is a strong negative correlation between sediment size (ranked from coarse to fine) and slope of the beach among these samples ($r = -0.944$, 18 d.f.; $P < 0.001$), in which d.f. indicate degrees of freedom (see Figure 7). Fine particles tend to be deposited at

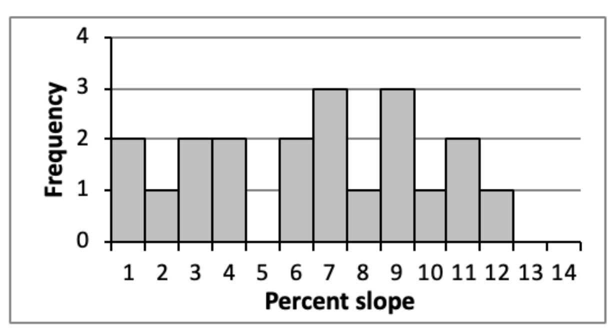

Figure 5. Frequency distribution of foreshore slope values measured at 20 randomly sampled points on the beach at San Miguel (mean 7.00%).

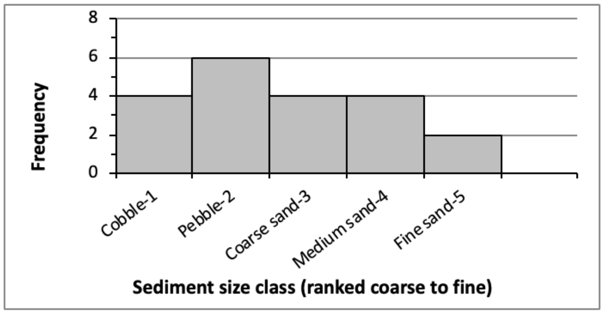

Figure 6. Frequency distribution of sediment particle size at 20 randomly sampled points. Pebbles were the most frequently observed size class.

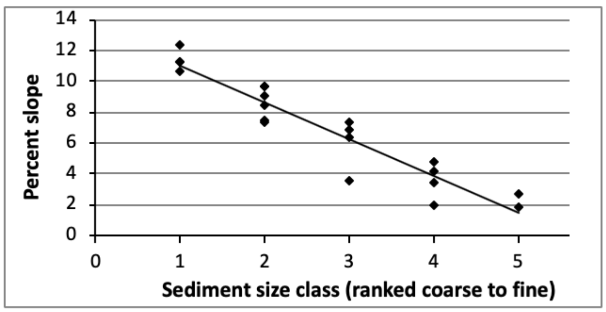

Figure 7. Relationship between sediment particle size, ranked from coarse (1=cobbles) to fine (5=fine sand), and the slope of the foreshore based on 20 random samples at San Miguel. There is a negative correlation between the two variables (r= -0.944, 18 d.f; P<0.001); larger particles are deposited in steeper beach profiles.

lower angles than coarse particles; the largest size class (cobbles) had the steepest beach profiles.

In the 20 replicate samples, a total of 1049 seeds were collected (range 1-390.5 per sample). Of these, 787 seeds (75.0%) were almendro, and the remaining 253 seeds belonged to other species. The density distribution per sample is shown in Figure 8a for seeds of all species (mean 52.4, variance 7784.38) and in Figure 8b for seeds of almendro alone (mean 39.4, variance 4233.37).

The spatial dispersion pattern for seeds among the samples was analyzed by comparing the ratio of variance/mean for the n samples to the expected value (1.00) for a Poisson distribution; the Poisson distribution is the expected, null distribution for objects dispersed in a random pattern. The comparison was done using a special t-test (Greig-Smith, 1983):

$$t = \frac{(variance \,/\, mean) - 1)}{[\,2\,/\,(n-1)\,]\,½}$$

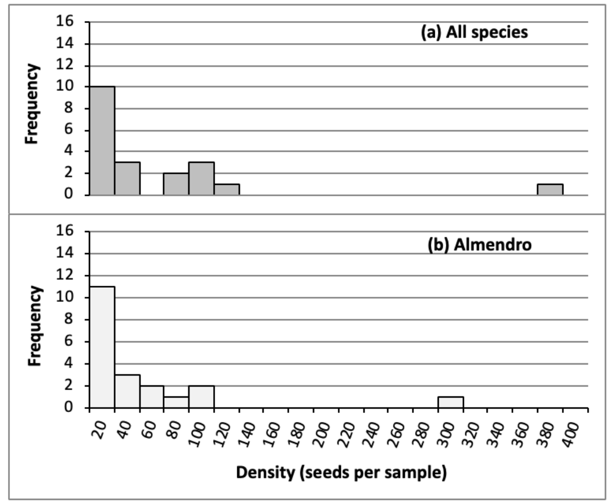

Figure 8. Frequency distribution of the number of seeds per sample for 20 samples of drift seeds. Above, seeds of all species (mean 52.4, variance 7784.38); below, almendro seeds alone (mean 39.4, variance 4233.37). The dispersion among samples in both cases is non-random, showing a clumped pattern. Seeds are not distributed independently of one another, but tend to occur in clusters or groups.

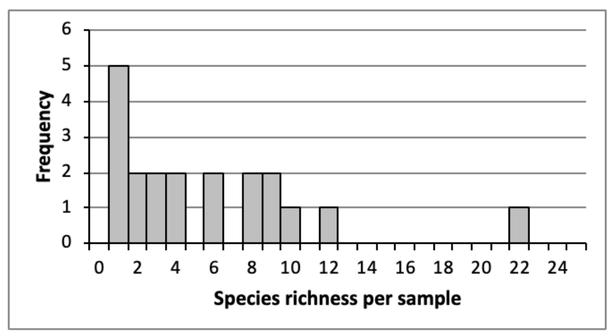

Figure 9. Frequency distribution of species richness of drift seeds in each of 20 samples. Values ranged from 1-22; the mean richness was 5.7 species.

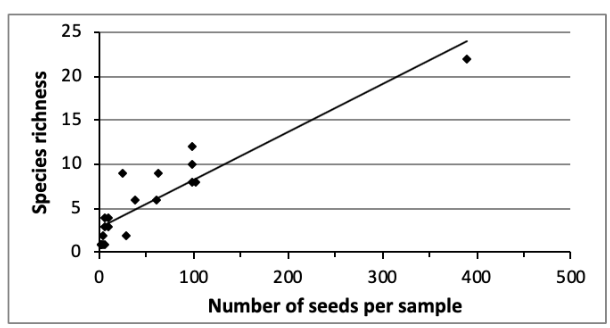

Figure 10. Scatterplot showing species richness as a function of the number of seeds in the sample. The two variables are highly correlated (r=0.917, 18 d.f.; P<0.001).

The dispersion in both cases is non-random, showing a clumped pattern. Seeds are not dispersed independently of one another on the shore, but occur more often than expected in clusters. The frequency distribution of species richness of seeds is shown in Figure 5. Richness ranged from 1-22 species per sample, with a mean of 5.7 species (see Figure 9). Species richness is highly correlated with the number of seeds present in the sample (see Figure 6). Samples with more seeds tended also to have more species represented (r=0.917, 18 d.f.; P<0.001) (see Figure 10).

The frequency distribution of seed size is shown in Figure 11a for all seeds of all species in the 20 samples (n=1049). Length ranged from 0.4-24 cm (mean 4.14 cm). The size distribution is shown in Figure 11b for seeds of all species exclusive of almendro (n=253), and in Figure 11c for seeds of almendro alone (n=787).

The mean seed length per sample was calculated for all species combined (see Figure 12a) and for almendro seeds alone (see Figure 12b). Mean length per sample for all species ranged from 3.0-6.1 cm (mean 4.39), and for almendro seeds alone ranged from 3.4-6.1 cm (mean 4.72 cm). The two

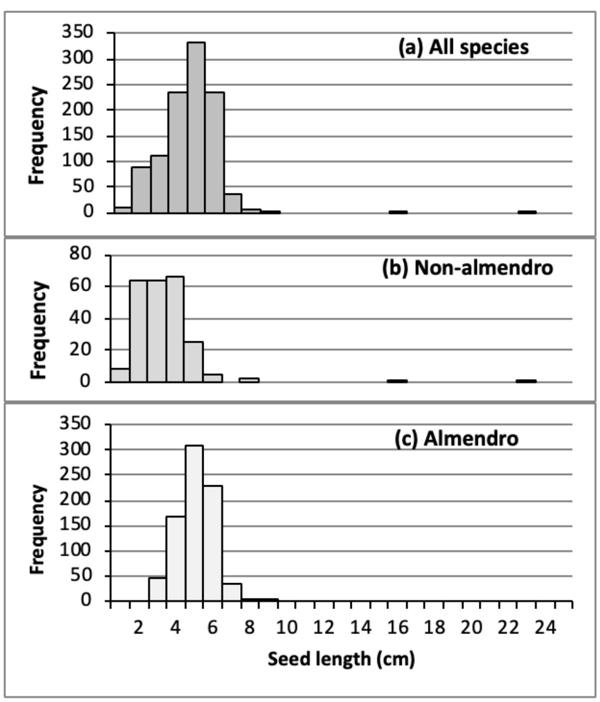

Figure 11. Frequency distribution of the seed length (all samples pooled) for seeds of all species (above), n=1049; all species exclusive of almendro (center), n= 253; and almendro alone (below), n=787.

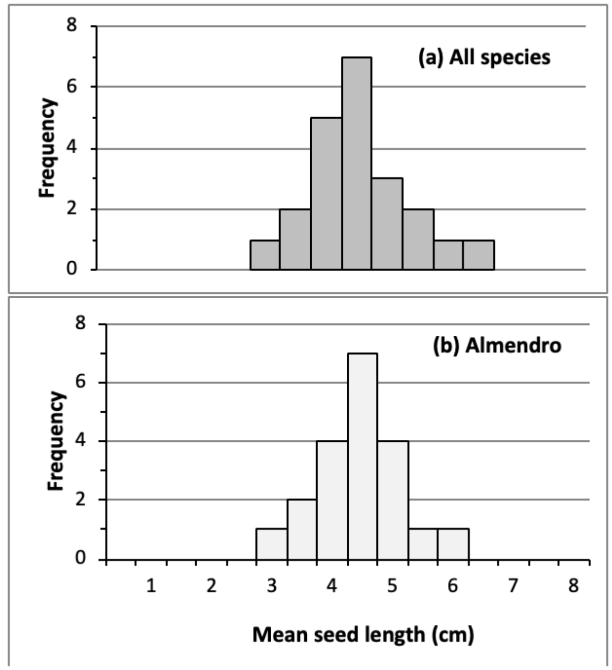

Figure 12. Frequency distribution of the mean length of seeds per sample for 20 samples of drift seeds. Above, seeds of all species (mean 4.39 cm); below, almendro seeds alone (mean 4.72 cm). The two size distributions are quite similar, as almendro makes up a large proportion of the total seed pool in each sample.

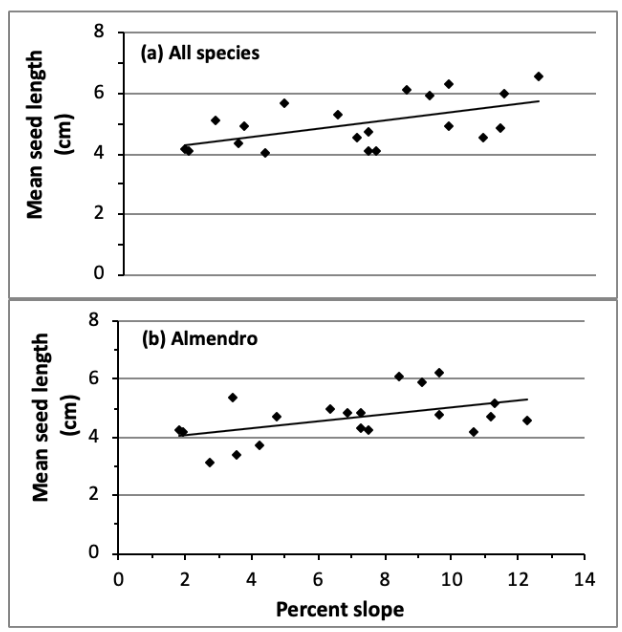

Figure 13. Scatterplot showing relationship between percent slope of the beach and the mean length of seeds per sample, for all species (above) and for almendro seeds alone (below). There is a positive correlation between the two variables in both cases (all species, r=0.549, 18 d.f.; P<0.05; almendro alone, r=0.473, 18 d.f.; P<0.05). Larger seeds tend to be found on steeper slopes.

distributions are very similar, as almendro seeds represent such a large proportion of the total seed sample.

The relationship between the percent slope of the beach and various aspects of seed deposition were analyzed. There is no correlation between beach slope and the total number of seeds per sample ($r=0.413$, 18 d.f.; $P>0.05$); the total seed density is independent of beach slope.

The mean length of seeds per sample is positively correlated with the percent slope of the beach (see Figure 13); the relationship is seen when all species of seeds are included ($r=0.549$, 18 d.f.; $P<0.05$) and also when only almendro seeds are included ($r= 0.473$, 18 d.f.; $P<0.05$). Larger seeds tend to be found at sites with steeper slopes. There is no correlation between beach slope and either the minimum length of seeds per sample ($r=0.226$, 18 d.f.; $P>0.05$) or the maximum length of seeds per sample ($r=0.349$, 18 d.f.; $P>0.05$). Both the minimum seed size and maximum seed size at these sample sites are independent of percent slope of the shore.

As is seen in Figure 14, the sediment size class (ranked coarse to fine) is negatively correlated with the mean size of seeds in the sample ($r=-0.450$, 18 d.f.; $P<0.05$). Larger seeds tend to be found at sites with larger particle size. There was no correlation between sediment size and either maximum seed size per sample ($r=0.286$, 18 d.f.; $P>0.05$) or minimum seed size per sample ($r=0.166$, 18 d.f.; $P>0.05$).

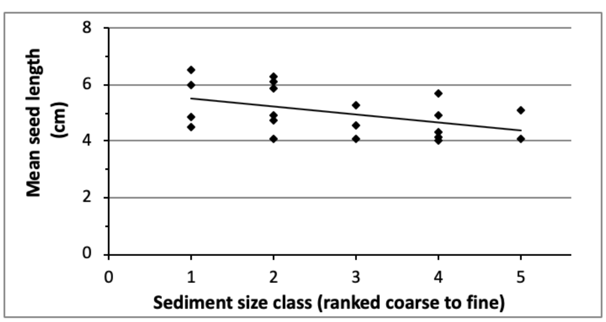

Figure 14. Scatterplot showing relationship between sediment particle size, ranked from coarse to fine, and the mean length of seeds in the sample (all species included). The two variables are negatively correlated ($r= -0.450$, 18 d.f; $P<0.05$); larger seeds are found at sites with larger particle size.

Discussion

The results of this study confirm that patterns seen at continental scales relating angle of deposition to particle size are clearly in play at scales of a few tens of meters.

Many details of hydrology and ocean currents along this shore remain unknown. The variability in wave energy, while not measured, can be inferred from the marked variation in foreshore slope and sediment size seen over even short distances. Previous studies have shown that seeds of tropical plants can be moved by ocean currents to new destinations, and the abundance and diversity of seeds arriving in a small area on the shores of San Miguel are evidence of that process (Nathan et al., 2008; Smith, 1990). Almendro, which was the most common species in the drift seed samples, is the most common species in the forest bordering the shore at San Miguel, suggesting that inputs of these seeds have been a long-standing process.

The number of seeds varied widely from sample to sample, but the number was not related to beach slope. The count of seeds present in the drift line may be affected by factors which are independent of beach profile. Rates of arrival on the beach could involve chance processes, such as the number of floating seeds which happen to be near the shore at any given time. The seeds present at a sample point may include accumulated seeds from past tides. Seeds may also be removed by animals after they arrive on shore. Almendro seeds in particular are favored by hermit crabs, harlequin crabs, squirrels, agoutis, and white-faced capuchin monkeys, and the drift lines themselves may be disturbed by digging of scavengers, such as coyotes, raccoons, and coatis (D. Lieberman, personal communication, July 2018).

The species richness per sample was recorded. However, species identifications (except for almendro) were not cross-referenced between samples; hence, it is not possible to determine the total species richness for seeds collected.

The clumped dispersion pattern of seeds implies that wave action along the shore is sufficiently variable to deposit seeds in a non-random pattern, with some spots receiving far more and others far fewer than would be expected by chance. It is doubtful whether this clumped pattern affects the distribution of germinated seedlings and adult trees along the shore. Characteristics of wave action and shore morphology are dynamic, and the patterns of deposition may change from season to season and year to year.

Patterns of seed dispersal on this shore are generally similar to patterns of sediment deposition. Seed size was not independent of sediment size. The conditions that led to the deposition of coarser, heavier particles also led to the deposition of larger seeds. This finding is reinforced by the correlations between sediment size and beach slope and between seed size and beach slope, in which larger particles were associated with steeper beach profiles. Perfect correspondence between sediment particle size and seed size seems unlikely, as rocks and seeds differ in terms of density and buoyancy. Without strong wave energy, sediments should tend to sink, while seeds, especially those capable of long-distance ocean dispersal, should tend to float. Thus, large buoyant seeds may be deposited in areas where large rocks are absent.

The pattern of beach profiles and sediment distribution were surveyed at a single point in time following a single high tide. The processes that shape the coastline are remarkably dynamic, and the characteristics measured must be in flux, shifting with daily cycles of high and low tides, lunar cycles of spring tides and neap tides, weather, storm events, and the seasons. Thus, the correlations observed in this study, most notably between percent slope and sediment distribution and between seed deposition and beach characteristics, must be constantly re-established and renewed over very short time periods.

The study was carried out during the rainy season, at a time with heavy surf and frequent storms. The specific findings of the study, such as the slope of the beach, the frequency of sediment classes, and the species composition, density, and sizes of seeds, might differ if the work were done at a time of calm weather during the dry season. However, the relationships between sediment size, slope, and seed size might still be present. Studies of these variables at other times and seasons would be of interest.

Acknowledgments

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